NOTES ON THE GENUS GASTROPILA

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The name Gastropila is applied by Honrich and Wright (1973) to Spegazzini's (1921) former genus Pila because his name, previously used in the Chlorophyceae, could not be admitted.

Spegazzini based Pila on the collection by Gaudichaud in 1835 near Montevideo, Uruguay, and identified by Leveille (1844) as a new Mycenastrum, M. fragilis Lev. This species also has been considered a Scleroderma by deToni (1888) and as Mycenastrum by Clemens (1931) and by Šebek (1958).

Honrich and Wright considered Gastropila to be monotypic, with G. fragilis (Lev.) Honrich & Wright as its only species. I am extending the concept of the genus to include four species previously considered to be Calvatias; these are C. pachyderma (Peck) Morgan sensu Coker and Couch (which I consider to be a synonym of Gastropila fragilis), C. fumosa Zeller, C. subcretacea Zeller, and C. hesperia Morgan.

The name Calvatia pachyderma (Peck) Morgan used by Smith (1964) and others involves a misunderstanding about the species described by both Peck and Morgan. As Lloyd (1904) pointed out, Morgan (1890), the first to use the combination Calvatia pachyderma, actually described C. lepidophora (E. & E.) Coker & Couch, not Peck's Lycoperdon pachydermum. Consequently, the author citation is incorrect. Kembly & Lee (1936) used this incorrect authority and copied Morgan's description, which is of C. lepidophora. Coker and Couch (1928) called this species C. pachyderma (Peck) Morgan, correctly describing the true C. pachyderma, based on Pringle 74, Santa Catalina, Santa Rita Monument, Arizona (FH, NYS), and noting the differences between C. pachyderma and C. lepidophora, following the opinion of Lloyd.

Lloyd (1916) was the first to call attention to the similarity between C. pachyderma and Gastropila fragilis, comparing material collected by Espinosa in Chile and material previously collected by Yates in California. Spegazzini was of the same opinion and put C. pachyderma into synonymy with Pila fragilis.

When I observed the spores and capillitium of the type of G. fragilis with the scanning electron microscope, I was struck by the similarity of this material to the spores and capillitium of C. pachyderma (fig. 1), and comparison of the peridia of these two species led me to the conclusion that they were not only similar, but that they are conspecific.

The specific name fragilis of Leveille takes precedence over pachydermum of Peck (1882), and I am putting Calvatia pachyderma (Peck) Morgan sensu Coker & Couch in synonymy with Gastropila fragilis (Lev.) Honrich & Wright.

The center of dispersal of the genus Gastropila may have been in the deserts and mountains of western North America, where several species developed, and the migration to the south may have occurred in recent (Pleistocene) geological times by way of the mountains, accepted by several authors, or by the Andes of Chimu, as Steinmann (1929) suggested, or by long distance dispersal (wind, birds, etc.). The distribution of G. fragilis seems to lend credence to the theory of Raven and Axelrod (1974) that the disjunct ranges (such as that of Larrea and others) between the North American desert regions and the mountains of temperate South America were almost certainly attained by such long-distance dispersal.

Key to the species of Gastropila

Exoperidium smooth.

Capillitium with round pits . . . . . G. fragilis.

Capillitium with slitlike pits.

Spores echinate . . . . . G. fumosa.

Spores smooth, with hyaline envelope . . . . G. hesperia.

Exoperidium with polygonal warts . . . . . G. subcretacea.

GASTROPILA FRAGILIS (Leveille ex Spegazzini) Honrich & Wright, Mycologia 65(4): 781. 1973.
Mycenastrum fragilis Leveille, Ann. Sci. Nat. Paris: Ser. II: 167. 1844.
Lycoperdon pachydermum Peck, Bot. Gaz. 7: 54. 1882.
Calvatia primitiva Lloyd, Letters No. 1: 2. 1904 (nom. nud.).
Pila fragilis (Lev.) Spegazzini, Rev. Chilena Hist. Nat. 25: 77. 1921.
Calvatia pachyderma (Peck) Morgan sensu Coker & Couch, Gast. East. U. S. and Can. 60. 1928 (not C. pachyderma (Peck) Morgan, J. Cinc. Soc. Nat. Hist. 12: 167. 1890 = Hypoblema lepidophora (Ellis & Everhart) Lloyd).
Langermannia pachyderma (Peck) Kreisel, The Genus Bovista. Beihefte Zur Nova Hedwigia Heft. 25: 202. 1967.

Basidiocarps 12-20 cm. in diameter, globose to subglobose, depressed above and slightly nippled below, attached below by a pinched base; peridia double, exoperidium white when young, brownish in age, smooth to lightly furfuraceous, scaling away, endoperidium very thick, 3-5 mm. wide, hard, rigid, fragile, tan but weathering white, corky-spongy internally, dehiscing by cracking or splitting of the upper part and forming large plates which fall away to expose the gleba; gleba

without sterile base, dark olive brown, exhibiting lysis when ripening but becoming powdery and blowing away, leaving the empty peridium shell; capillitium formed by branching threads 4.5-7.5 µ in diameter, the branches Y-shaped, walls thick, dark olive brown, septate, breaking at the septa, pitted, pits round, sometimes partially perforating the walls; spores 3.5 x 5.5 µ in diameter, smooth, ovoid with a very short stump or pedicel, with a guttula, yellowish to brown.

TYPE: Mycenastrum fragilis Leveille, Gaudichaud s.n., Montivideo (1835). (P).

Habitat: In North America, on soil in open places, in arid regions, and in the mountains in the West. In South America, on soil among grasses, in open places.

Distribution: Western North America (Colorado, Arizona, California); South America (Uruguay, Argentina, Chile); Iran; Australia.

Specimens examined: AUSTRALIA: South Australia, Adelaide, Cleland 904 (Lloyd 3043) (BPI). CHILE: Santiago, Spinosa 4 (Lloyd 32415) (BPI); Los Perales, Spegazzini 15917 (as Bila fragilis (Lev.) Speg.) (LP). IRAN: Khorason Mont Ku-e Bizg, Swobada s.n. (Rechinger 2492) (BPI,NY). MEXICO: Hidalgo, Cerro Santa Ana, Guzman 3843 (ENCB); Villa Juarez, Adalanta, Dudley s.n. (BPI). UNITED STATES: ARIZONA: St. Rita Monument, Santa Catalina Mountains, Pringle 74, type (NYS), Auth. mat'l. (FH) part of the type (BPI, NCU, NY); Santa Catalina Mountains, Long 7949 (BPI); Prescott, Long 7884 (BPI). CALIFORNIA: Sin. loc., Dudley 56 (NYS), 309 (NCU, NYS), Morse s.n. (NCU), Yates s.n. (Lloyd 32414) (BPI), Long 7749 (BPI); Alameda County, McCabe s.n. (MICH); Berkeley, Copeland M-618B (as Calvatia sp.) (BPI), Hickey s.n. (BPI), Long 8059 (BPI), Mentzer s.n. (ex Herb. Berkeley) (FH); Berkeley Hills, Morse s.n. (NCU); Contra Costa Co., Bowerman 3772 (ex Herb. Univ. Calif.) (FH); Humboldt Co., Lamphere s.n. (as C. lampherae Weber & Smith, note in Herb. 1972) (MICH); Branstolter Ranch, Arcata, Lamphere s.n. (MICH); Kentfield, Mattel M-82 (BPI); Las Pocetas, Sur, Nanthera s.n. (FH); Los Angeles, Towne s.n. (Lloyd 22588) (BPI); Marin Co., Reyes, Barbour s.n. (ex Herb. Myc. Soc. Berk. Cal.) (NCU); San Francisco Bay Region, Parks s.n. (BPI, NCU), M-8d (BPI), Rea H-230 (MICH); Monterrey, Ashley s.n. (Long 8060) (BPI); Pacific Coast, Morse s.n. (NCU); Santa Barbara Co., Rea H-1034 (= C. californica Weber & Smith, Note in Herb. 1972 (MICH), Rea s.n., 231, H-202, H-203, H-1440 (MICH); San Bernardino, Parish s.n. (Lloyd 32411) (BPI); Santa Clara, Gibray, Appel s.n. (ex Herb. Myc. Soc. Berk. Cal.) (NCU); Santa Catalina Island, Nuttall 502 (Lloyd 32410), 503 (Lloyd 32409) (BPI), Trask s.n. (Lloyd 32412), Trask s.n. (Lloyd 32413) (BPI); San Francisco Co., Barbour s.n. (BPI), Reyes, Lighthouse s.n. (BPI), Tiburon, Hickey s.n. (Long 8058) (BPI). COLORADO: Denver, Bethel s.n. (BPI, NCU). IDAHO: Smith's Ferry, Weir 8129 (Lloyd 32408) (BPI). NEW MEXICO: Doña Ana Co., Cambel s.n. (Long 8291) (BPI). SOUTH DAKOTA: Huron, Crouch s.n. "probably Langermannia gigantea" (BPI). UTAH: Salt Lake Co., Garrett 534 (NCU, NYS). WASHINGTON: Yakima, Brandegee s.n. (BPI).

Discussion: This species, already notable for its anatomy, is also most interesting in its ecology. Its presence in two localities so far apart from each other in a north-south position on the American continent is an example of amphitropical distribution of a species. Although some flowering plant families and/or genera have parallel distribution, species occurrences in the temperate zones of both American continents (the North American range being limited in most species, as in our fungus, to the western deserts and mountains), such as Bowlesia incana Ruiz & Pavón in the Umbelliferae, and Nama dichotomum (R. & P.) Choisy (Hydrophyllaceae) are rare.

In checking the Field Museum herbarium for flowering plants cited by Constance (1963) as having amphitropical distribution, I was struck by the similarity of collection data of Bowlesia incana and C. pachyderma (= Gastropila fragilis). Pringle's type of C. pachyderma was collected in the Santa Catalina Mountains near Tucson, Arizona during his collecting trip of 1881 for flowering plants; among the plants he collected that year is a specimen of Bowlesia incana from the same area. There are also collections of both B. incana and C. pachyderma made by Parish in the Tucson area. I also found in our herbarium, collections of B. incana from Pakistan, and there are specimens in New York and in the Lloyd Herbarium (BPI) of C. pachyderma from Iran. Constance also cites collections of B. incana from New Zealand and Australia, and there are specimens of C. pachyderma in the Lloyd Herbarium (BPI) from Australia.

GASTROPILA FUMOSA (Zeller) P. Ponce, comb. nov.
Calvatia fumosa Zeller, Mycologia 39: 300, f. 10. 1947.
Calvatia fumosa var. idahoensis Zeller and Smith, Lloydia 27(3): 156. 1964.

Basidiocarps 3-10 cm. in diameter, subglobose to depressed-globose, attached below by a white, cordlike rhizomorph; peridia double, exoperidium white to sepia or brownish, smooth to slightly furfuraceous, becoming wrinkled to plicate in drying, sometimes falsely areolate, endoperidium thick, 1-2 mm. wide, hard and persistent, white, dehiscing by the splitting of the upper part; gleba without sterile base, dark brown, becoming very powdery and completely falling away at maturity; capillitium formed by branching threads 4-11 µ in diameter, usually in long segments, sparsely branched, the branches Y-shaped, the walls even, irregular, or with knoblike projections, walls 1-1.5 µ thick, rupture borders of the segments with irregular edges, dark olive-brown, aseptate, pitted, pits slitlike; spores 4-7 µ in diameter, globose to subglobose, echinate to verruculose, often 1-guttulate, dark brown, with a short or rudimentary pedicel.

TYPE: C. fumosa Zeller, F. P. Sipe, s.n., Crater Lake National Park, Oregon (NY).

Habitat: Solitary to gregarious under spruce and fir in the mountains during the summer and early fall.

Distribution: Arizona, California, Idaho, Oregon, Washington, Wyoming.

Specimens examined: ARIZONA: Kaibab Nor. Forest, Long 1807 (BPI); Josephine County, CLND 157 (MICH); Lane County, Sipe s.n. (MICH); Klamath County, Cooke s.n. (MICH). CALIFORNIA: Sin. loc., Cooke 32561, 32579, 34231 (MICH); Mt. Shasta, Cooke s.n., 32561 (BPI), 20050, 29512, 30057, 32561, 32598, 34231 (UC), 32645 (CINC); Siskiyou County, Cooke 16799 (NY), 35086, 37284, 39271 (MICH); Spruce Cave, Trinidad, Parks 8122 (NY); Lassen Volcanic National Park, Cooke 30037, 37132 (UC), Cooke 42744, 42793, 42832, 42859, 42917 (CINC). COLORADO: Sin. loc., Grandall 353 (as Lycoperdon cerebriforme) (FH). IDAHO: Adams County, Hell's Canyon, Bigelow & Smith 45279 (Type of C. fumosa var. idahoensis); Smith 46012, 60311 (MICH); Bonner County, Priest River, Smith 67879, 67882, 67965, 68645, 71347 (TYPE) (MICH); Idaho County, Rust 959 (NY), Trueblood 2346, 2546, 2566, 2601 (MICH), Smith 2538 (as C. fumosa var. idahoensis), 6921 (as C. fumosa var. idahoensis), 38390, 45358, 47591, 58644, 58647, 58911, 59453, 59455, 60019, 65294, 68114, 68116, 68166, 68858, 68859, 68861, 68863, 68986, 69251, 69864, 70656 (MICH); Bergfort, Smith 68984, 68985 (MICH); Upper Payette, Smith 69904 (MICH). OREGON: Sin loc., Trappe 22 (MICH), Trueblood 1062 (MICH), Zeller 15522, 15630, 15778 (NY); Blue Mt., Cooke 204 (BPI), 25319 (FH, NY, UC); Crater Lake National Park, 20482 (BPI), Cooke 24082 (UC); Anne Spring, Pul Camp, Cooke 340 (NY), Sipe s.n. (Type) (NY); Clackamas County, Smith 27143 (MICH); Lane County, Gold Lake, Trappe 586 (BPI, MICH, NY). UTAH: Duchesne County, Dublin 2698 (McKnight 2709) (BPI); Mirror Lake, McKnight F3027 (BPI); Lost Lake, McKnight s.n. (BPI); Smith County, Lily Lake, Dublin s.n., 2603, 2634 (BPI); Summit County, Fish and Game Cabin, McKnight MVD2334, MVD2474, Lake Summit, 1326; Wallow National Park, Cooke 25273 (UC); Washington Lake, Duke, McKnight F5235 (BPI), F6474 (BPI, NY); Utah County, Skyline Drive, Provo River, McKnight F5389 (BPI). WASHINGTON: Sin loc., Bigelow 47751 (MICH); Pierce County, Smith 28900, 28968, 28982, 29220, 31363, 31382, 47589, 47591, 47725, 47758, 48853 (MICH); Valley County, Smith 44308, 44309, 44351, 44634, 44638, 44722, 44777, 44866, 45067, 45202, 45236, 45245, 45320, 45329, 45339, 45348, 45416, 45420, 45861, 45910, 46494, 46673, 48247, 58378, 58410, 58457, 58473, 58566, 58609, 58692, 58740, 58762, 58763, 58783, 58844, 58993, 59102, 59216, 60227, 60292, 64929, 64958, 64963, 65086, 65306, 65435 (MICH). WYOMING: Sin. loc., McKnight F7912 (MICH); Albany County, Smith 34596, 34640, 35389, 34815, 35474, 35591, 36240, 36242, 36243 (MICH), Solheim 3889, 3390 (MICH), Thiers 84 (MICH); Carbon County, Medicine Bow Mountains, Cooke 26927 (BPI), Couch 14687 (NCU); Teton County, McKnight s.n. (BPI); Teton National Park, McKnight 10320 (BPI); Yellowstone National Park, McKnight F917, F1717, F7713, F7727, F7843, F7912, F7973, F8096, 10466 (BPI).

Discussion: This species presents the obvious characters of the genus, such as the hard, thick endoperidium, almost inseparable from the exoperidium, and the absence of subgleba (which separates this group from the true Calvatias).

The range of G. fumosa in North America, like that of G. fragilis, is restricted to the western mountains. It also shares the same habitat with G. subcretacea, reaching maturity at the same time.

Smith (1964), also recognizing the similarity of this species and G. subcretacea to G. fragilis (based on gleba color and the hard peridial wall), placed them all in the same stirps.

GASTROPILA HESPERIA (Morgan) P. Ponce, comb. nov.
Calvatia hesperia Morgan, J. Cinc. Soc. Nat. Hist. 18: 39, plate II, f. 9. 1895.

Basidiocarps 4-8 cm. in diameter, subglobose, depressed, white to gray, attached below by a pinched base; peridia double, the two layers closely knit together, hard, coriaceous, exoperidium hyaline or white, endoperidium thick, about 0.5 mm. wide, rigid, tough, persistent, dehiscent by an irregular, torn aperture; gleba without sterile base, compact and firm, clay color to ochraceous; capillitium formed by very long threads, 6-8 μ in diameter (once or twice the thickness of the spores), scarcely branched, the branches Y-shaped, remotely septate, breaking easily at the septa, walls thick, pitted, the pits slitlike, sometimes partially perforating the walls; spores subglobose or ovoid, 4.5 x 5.5 μ in diameter, brown, very indistinctly warted (almost smooth), hyaline envelope present, with a minute pedicel.

TYPE: McClatchie s.n., Pasadena, Calif., 1895 (NY).

Habitat: Sandy soil.

Distribution: California.

Specimens examined: CALIFORNIA: Pasadena, McClatchie s.n. (Type) (NY); San Francisco, Eastwood 8 (Lloyd 22578) (BPI); Claremont, Crawford E-4 (Lloyd 22579) (BPI); sin loc., Morgan 3073 (Lloyd 22580) (BPI); Pasadena, Weck s.n. (NY).

Discussion: Morgan compared this species with Bovista pila B. & C., but said that the basidiocarp of the former was 4-8 cm. in diameter. Our species resembles Gastropila fragilis, which has affinities in the inseparable peridia, but ours differs in the capillitium with

its slitlike pits. G. hesperia, which also resembles G. fumosa in the peridia and the slitlike pits of the capillitium, but has the spores almost smooth and with a hyaline envelope, may be distinguished from both G. fragilis and G. fumosa by its much wider capillitium threads.

GASTROPILA SUBCRETACEA (Zeller) P. Ponce, comb. nov.
Calvatia subcretacea Zeller, Mycologia 39: 298, f. 6. 1947.

Basidiocarps 12-20 cm. in diameter, depressed-globose to pulvinate, attached below by white mycelium; peridia double, exoperidium white with polygonal warts, the tips of which are often smoky gray, the warts 7 mm. across, sometimes marked with parallel lines at various heights, these converging at the apex, never connivent, breaking away individually at maturity, endoperidium thin, firm, furfuraceous, honey yellow, breaking irregularly at the upper part; gleba without sterile base, at maturity burnt umber, powdery and falling away; capillitium formed by branching threads 2.5-10 µ in diameter, elongate, flexuous, the branches Y-shaped, aseptate or septa very rare and then breaking at the septae, rupture borders of the segments with irregular edges, walls even to sinuous, or tortuose at the ends, 1-2 µ thick, brown, pitted, the pits slitlike to tear-shaped, often abundant; spores 3.5-6.5 µ in diameter, globose, smooth or asperulate, hyaline envelope often evident, often 1-guttulate, brown, with a short pedicel.

TYPE: C. subcretacea Zeller, J. R. Kienholz s.n., Cloud Cap Inn, Mt. Hood, 1936, Hood River County, Oregon (BPI).

Habitat: Solitary or scattered under spruce and fir in the mountains during the summer and fall.

Distribution: California, Oregon and Idaho.

Specimens examined: CANADA: Labrador, Port Lawian, Morse s.n. (BPI). UNITED STATES: ALASKA: Cape Lizburne, Mason s.n. (BPI). CALIFORNIA: Sin loc., Cooke 32644, 33492, 34128, 34974, 34996, 37168 (NY); Shores of Lake Alpine, Alpine County, Bonar s.n. (Herb. U.C. 960454) (UC); Fresno, Johnstone s.n. (as C. minima) (BPI); Janesville, Copeland s.n. (BPI); Lassen Volcanic National Park, Cooke 33491, 42860 (CINC); Mt. Shasta, Siskiyou County, Cooke 8671, 10222, 10238, 10272, 14742, 15650, 15665 (NY), 18111 (NY, UC), 18153, 18414, 30054 (UC), 32597, 32644, 42638 (CINC); Sequoia National Park, M.T. Cook s.n. (UC). IDAHO: Adams County, Smith 45278, 46772, 59146, 60293, 60316, 60317 (MICH); Boise County, Smith 58996 (MICH); Idaho County, Quimby 113A (MICH), Smith 58610, 58645, 58648, 58910, 59438, 60288, 68271, 68835, 68857, 68860, 68862, 69118, 69566, 69887, 71366 (MICH), Wehmeyer s.n. (MICH); Owyhee County, Smith 6500 (MICH); Boulder Lake, Smith 15825 (MICH, NY); Hell's Canyon, Smith 60312 (as C. fumosa) (MICH); North

Forest, Smith 15330 (MICH, NY); Valley County, Smith 15825, 15930, 23546, 44635, 44728, 44865, 44867, 44877, 44903, 45239, 45248, 45256, 45321, 45322, 45323, 45336, 45347, 45417, 45418, 45419, 45719, 45750, 45751, 46672, 58376, 58557, 58680, 58698, 58699, 58737, 58765, 58781, 58782, 59016, 59049, 59060, 59136, 59138, 59298, 59659, 64975, 65066, 65169, 65247, 65248, 65264, 65304, 65308, 65315, 65320, 65425, 65426, 65999, 66016, 66143. OREGON: Crater Lake National Forest, Sipe s.n. (NY); Josephine County, Smith 55617 (MICH); Oregon County, McKnight F5424 (BPI). WASHINGTON: Sin loc., Smith 68388 (MICH); Clallam County, Smith 14489 (MICH); Kittitas, Maas 2253 (BPI); Olympic Mountains, Smith 14489 (NY); Paradise Park, Mt. Rainier, Trappe 285 (BPI, NY).

Discussion: Zeller, who, in his discussion of this species, concluded that its closest affinities were with Calvatia cretacea, nevertheless recognized such important differences as ectoperidial color; size, color, and contouring of warts; endoperidial surface; and the absence of a sterile base. Further, he did not emphasize the fact that the warts of G. subcretacea are never fused as in C. cretacea; that the endoperidium of G. subcretacea is hard and difficult to separate from the exoperidium; that in C. cretacea, the capillitium is accompanied by membrane but in G. subcretacea, it is always clean; and that the subgleba (always present in C. cretacea) is wanting in G. subcretacea. The absence of the subgleba in G. subcretacea greatly influenced my decision to transfer the species from Calvatia to Gastropila.

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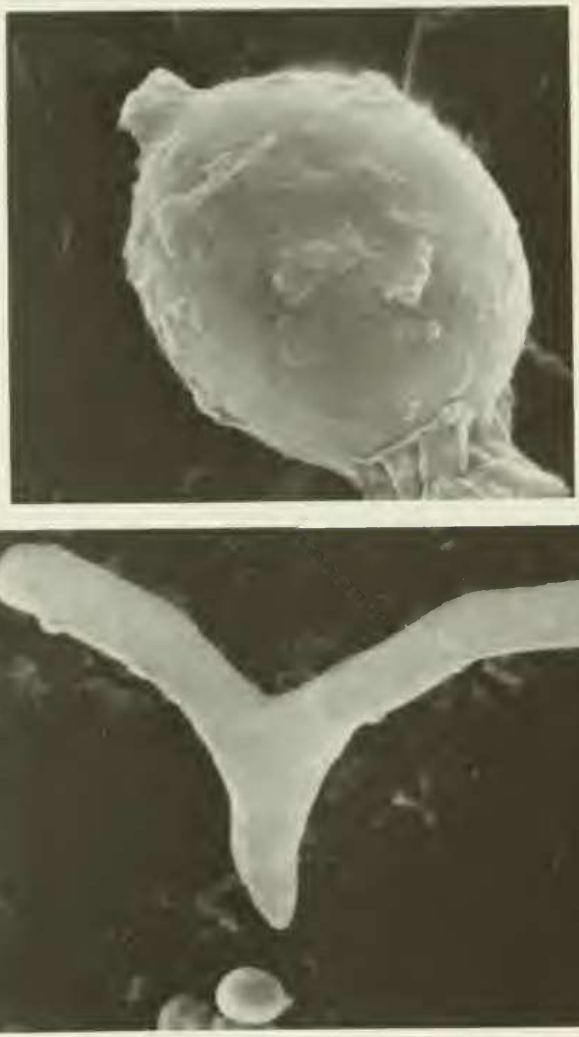
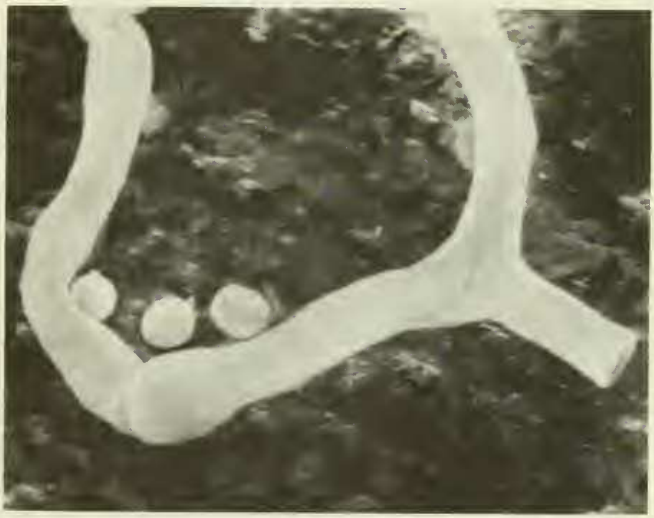


Fig. 1. Gastropila fragilis. A, Spore of the type, X 16,000; B, Capillitium and spores of the type, X 1,500.

A



B

Fig. 2. Calvatia pachyderma (= G. fragilis). A, Spore of the type, X 15,000; B, Capillitium and spores of the type, X 1,500.